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The influence of man and climate on dispersion patterns within a population of adult *Lasiommata megera* (L.) (Satyridae) at Brereton Heath, Cheshire (U.K.)

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Abstract

Mapping of adult *L. megera* in a local population at Brereton Heath, Cheshire, has revealed that : (i) the adults are not distributed evenly over the heath, (ii) the sexes differ significantly in their distributions, and (iii) the distribution of sexes changes substantially during the flight period ; – the males from north to south, the females from south to north. The overall dispersion of adults has been related to resources and land use, the distribution of sexes to their specific requirements for mate location and egglaying. Changes in the male distribution result from their gradual eclosion southwards as the season progresses rather than from dispersal, whereas changes in the female distribution probably relate to their avoidance of male harrassment once they have been mated. Some general comments are made on the limit to the northern and altitudinal distributions of the butterfly in Britain and to its capacity for extending its range as in recent years.

Introduction

An obvious and insidious trend, since the second world war in particular, has been the extinction and systematic decline in butterfly populations in Britain and elsewhere in western Europe (Thomas 1984 ; Heath *et al.* 1984). In Britain, although climate places restraints on butterfly species (cf. Dennis 1977, 1985), much of the decline is attributed to the surge in intensive land use and changes in land management (Thomas 1976-78 ; Thomas 1983a, Warren 1984 ; Heath *et al.* 1984). As a result, the last decade has witnessed a series of detailed local studies on individual species (*vide supra* ; Thomas and Simcox 1982 ; Thomas 1983b, Thomas 1974 ; Warren 1985 ; Dempster *et al.* 1976 ; Dempster 1971 ; Duffey 1968 ; Porter, 1981). The *raison d'être* of such intensive survey is that the factors influencing the production and survival of early stadia and the dispersion of individuals within habitats provide a key to understanding the distribution of the species over a wider area. Different factors have been found to be critical in different

species (cf. Dennis 1972a ; 1972b ; Pollard 1979 ; Courtney 1980 ; Ehrlich *et al.* 1975 ; Singer 1972 ; Douwes 1976).

The present survey, investigating the dispersion pattern of adult *L. megera* is unusual in at least two respects. First, it is one of the few species in Britain which has actually extended its range in recent years (Dunn 1974 ; Thomson 1980). In Cheshire, it is a common butterfly, in fact our only truly hedgerow and roadside Satyrid. Secondly, the survey at Brereton Heath shows that human interference need not always be detrimental to butterfly populations. *L. megera* extends its range a little further north than the southern Scottish coastline but is absent from higher ground as in the Pennines and the Lake District. The current survey developed from casual observations of discrepancies in the distribution of adults at a local scale on Brereton Heath.

Brereton Heath Country Park has been created out of an abandoned sand quarry. It comprises a lake (400 × 150 metres) surrounded by open ground, a belt some 50 × 150 metres wide, which is enclosed by birch and oak woodland to the south and east and by a line of trees and agricultural land to the north and west (Figure 1). The entire habitat (600 × 600 metres) forms an island on a fluvio-glacial sand base, isolated from other rough ground. Its catchment for the hundreds of summer visitors extends from the Potteries to Manchester and from Sandbach to Macclesfield, who arrive to picnic, walk, wind surf, fish canoe, and ride horses.

Methods

Data on adult *L. megera* have been obtained by linking a mark, release, recapture technique (MRR ; Ehrlich and Davidson 1960) to a fixed transect around the lake, along the length of the horse run and the adjoining road. The transect was devised to cover all the open ground. The location of all individuals captured and seen was marked on a large scale map (1 : 2,500) and their behaviour recorded. Additional data on behaviour have been obtained using a portable recorder (Dennis 1982). Oviposition sites and nectar sources have been mapped independently. *L. megera* is double brooded throughout Britain and most observations derive from detailed surveys on the second brood in August 1982 and 1983. Meteorological data for these periods have been obtained from Jodrell Bank. More detailed temperature and wind speed measurements have also been made. Wind speeds for different parts of the heath have been obtained by using two hand held anemometers, one standardized against a control placed at the entrance to the park. Temperatures (shade and exposed) were taken throughout one cloud-free day at two sites on the north and south lake banks, 5 cms over bare ground using identical instruments (calibrated), aluminium foil housings and

wood platforms. Population analysis of the MRR data has been by way of JOLLY, FISHER and FORD and the Lincoln index (BLOWER *et al.* 1981 ; BEGON 1979). A number of dispersal measures were used (cf. SCOTT 1975 ; SHREEVE 1981) but most (d_i, t_i, v_i, D, T, V) were found to be sensitive to sampling intensity (MRR events and recaptures) and to be useful only when comparisons are made in one study. Three measures were applied : R_T, the range in metres between first and last capture ; R_S, the maximal range or direct distance between the furthest points of capture (in both cases, the straight line distance is taken) ; and BATSCHELET's r index of directionality, $r = \cos(\theta/n)$, where θ is the angle between successive vectors of movement (BATSCHELET 1965).

Results

1. Dispersion Patterns

Negative areas : Generally both sexes of *L. megera* avoid shade and areas exposed to high winds. It is completely absent from the canopied woodland. In the main this comprises *Betula* with some *Quercus* including underlays of *Pteridium, Deschampsia flexuosa, Calluna vulgaris* and some *Vaccinium myrtillus.* It is also absent from dense high grass cover whether this comprises *D. flexuosa* or several grass species on which the larvae will normally feed ; such an area surrounding scrub to the north of the heath is frequented by *M. jurtina* instead. Similarly, both short mown grass areas and open plain areas of *Calluna* amid damp bare clay soils are avoided, the only *L. megera* here were seen to be crossing the area in a direct line (cf. Figure 1 with Figures 2-4). *Calluna* is not used as a nectar source by second brood individuals.

Positive areas : *L. megera* prefers sheltered sunny open areas amid broken terrain, where hummocks and hollows reduce wind speed, thus allowing the insect to raise its temperature (by basking) to appropriate levels (FINDLAY and FINDLAY 1983) as well as providing perch and oviposition sites (*vide infra*). Favourite habitats include road verges, hedgerows, banks, lines of fencing and paths – thus most of the surrounds of the heath. The lake bank, with its patches of bare ground, shrubs and broken terrain, as well as enclaves into the woodland, – those with bare ground, nectar sources and grass clumps – are also appropriate habitats. Nevertheless, the distribution of males differs significantly in detail from the distribution of females.

The males are primarily engaged in mate location and nectaring. Mate location behaviour involves both perching and patrolling, and shelter and sunlight are important for both of these activities. Thus, males typically patrol

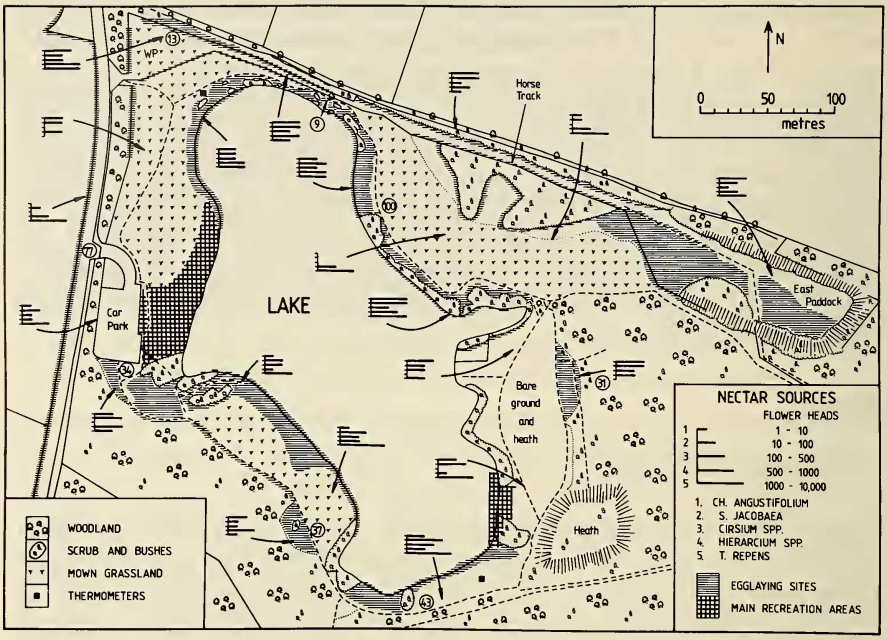

Fig. 1. Brereton Heath, illustrating vegetation zones, the main areas for recreation, egglaying sites and nectar sources (August 15, 1983). *S. jacobaea* and *Hierarchium* spp. are the most important nectar sources. The location of thermometers and anemometers for local climate measures are also shown. Wind speed is given for eight sites as a percentage of that for the maximum value recorded on the east bank (100) taken over 4 days in different wind directions.

on the lee side of hedges, depending on wind direction. Furthermore, mapping the precise location (0.5 metre resolution) of perches (for territories) at the north western entrance to the heath (952544) has shown that the microdistribution of adults changes from day to day in relation to wind direction. Most of the males are concentrated in the north western part of the heath (Figure 2 and 6), in the western paddock, which receives most sunlight and experiences the highest temperatures and lowest windspeeds (*vide infra*). Far fewer males are found on the east bank of the lake than the west. The east side is directly exposed to the prevailing westerlies, typically north westerly winds (see Figure 1). Nectar sources are ubiquitous throughout each brood and do not overly influence male distributions though movements occur between mate location sites and nectar sources, in particular between the western paddock and the northern lake side. Patrol lines or flyways (habitat edges) and perch sites are essential ingredients in male distributions. Bare ground, stones or other upstanding objects, fences and

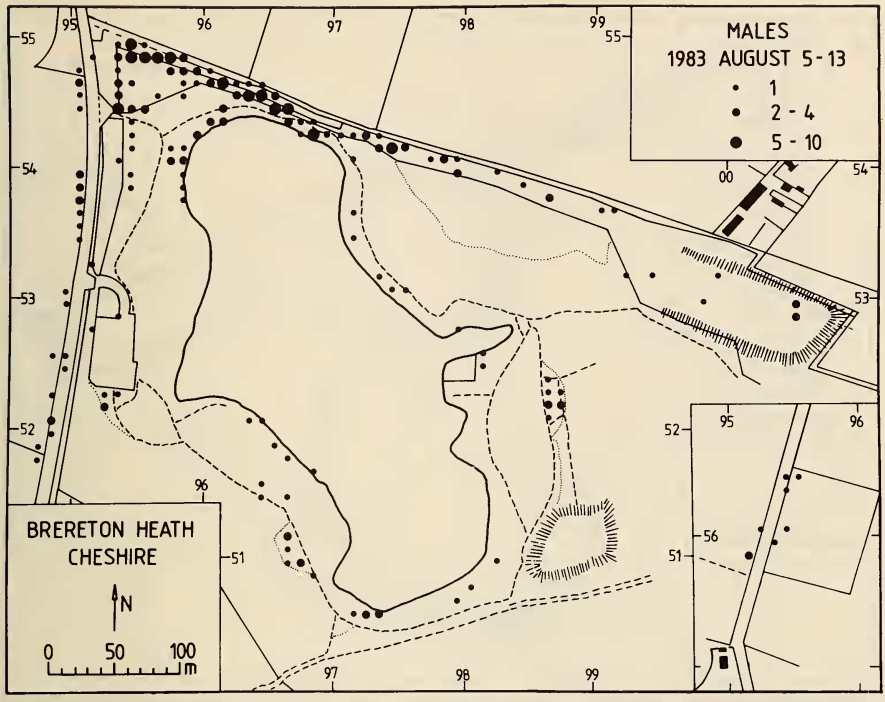

Fig. 2. The distribution of male *L. megera* for the period August 5-13, 1983.

hedges all provide prominent perch sites which are not afforded by open grass (Dennis 1982). Males are found wherever there are egglaying sites (Figure 1), but their predominance in the west paddock and sparseness on the north east lake side, where females congregate for nectaring and egglaying underlines sheltered, warm and sunlit areas as the major mate location cue. It is suggested that females seek out sunny, sheltered edge sites for courtship.

Although females adhere to similar terrain as males, there are striking differences in distribution. In particular, far fewer were recorded in the western paddock and along the horse run than expected and more along the north east lake bank, although the former areas are entirely suitable (and are used) as egglaying sites. Although *L. megera* is a grass feeder in the larval stage, females are nevertheless very particular about egglaying sites (Dennis 1983). Open mown grass areas and dense grass cover are ignored by them. Instead females select edge sites where the hostplants abut on some obstacle (hedge, fence, lake bank, indentations made by livestock or rabbits) or form a recess in their own right (grass clumps). Occasionally, the butterfly will lay

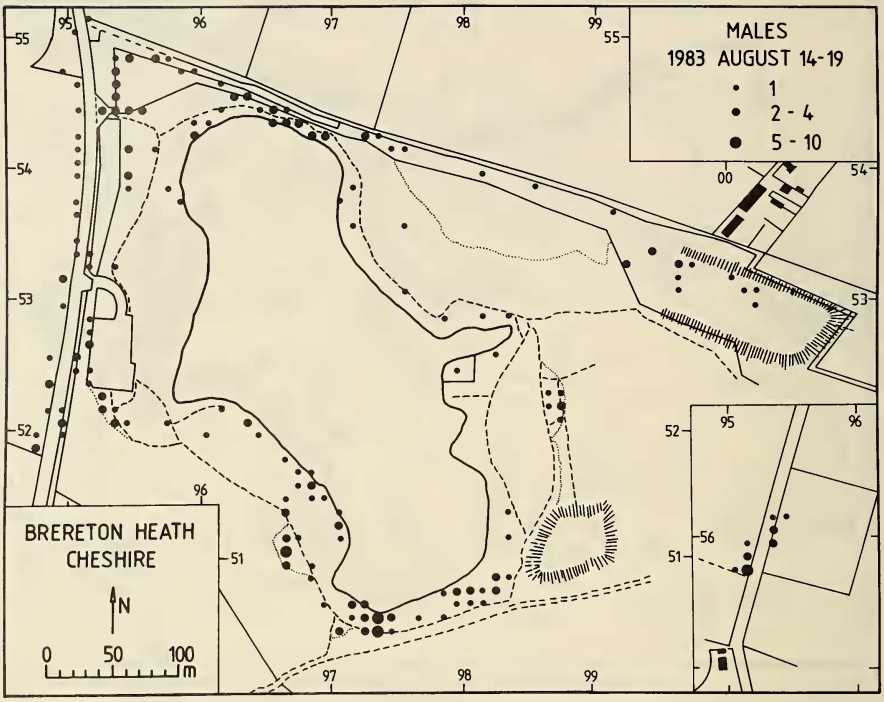

Fig. 3. The distribution of male *L. megera* for the period August 14-19, 1983.

where the hostplant is in patches amid bare sandy ground. The lack of females in the western paddock may well be due to male harrassment of females trying to lay eggs there, although some underrecording may well occur, as any unmated female will quickly receive a suitor in that area, and *in cop.* pairs, apparently well concealed, are rarely seen. Only some 10 pairs were recorded during the 1982 and 1983 seasons.

Females are opportunists and tend to congregate around the freshest nectar sources which are also close to oviposition sites (970538) where they intermittently engage in nectaring and egglaying.

2. Intra-brood changes in dispersion patterns

The most outstanding feature of *L. megera* dispersion of Brereton Heath is the change in adult distributions, particularly of males, during any brood. Mapping adults during the second broods of 1982 and 1983 has shown that males appear first in the north western paddock and then 'spread' southwards

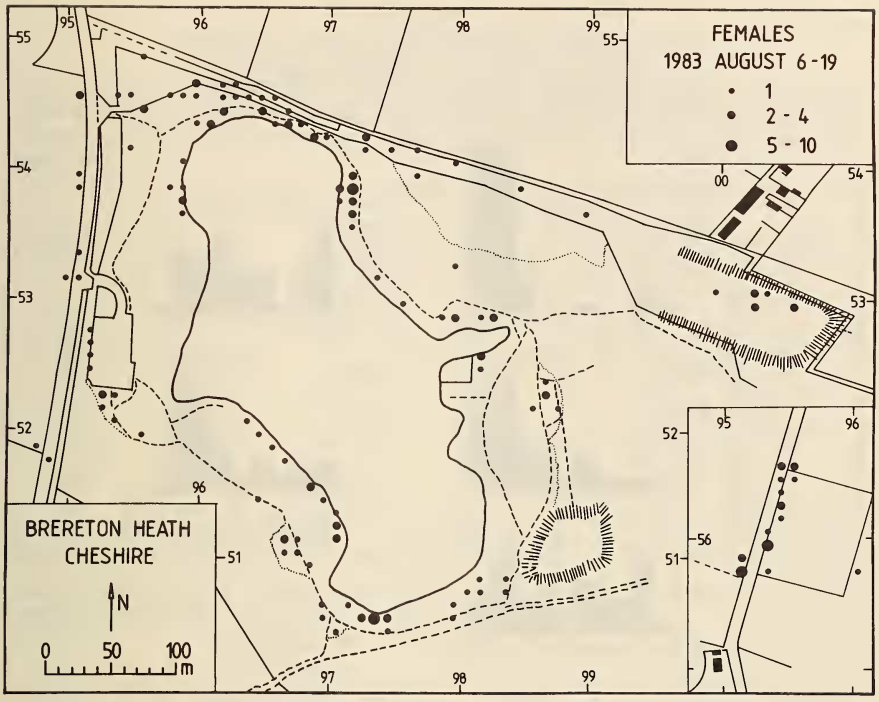

Fig. 4. The distribution of female *L. megera* for the period August 6-19, 1983.

as the season progresses and population increases (see Figure 2 and 3 ; Table 1). Early male and late male distributions differ significantly ($\chi^2_{(8)} = 87.4$; $p < 0.001$; see Figure 5). During the same period female distributions appear to change though less dramatically ($\chi^2_{(4)} = 12.25$, $p < 0.02 > 0.01$, see Figure 5). However, the changes in male and female distributions appear to be in opposite directions, the female distribution becoming more northerly as the season progresses. As such, the male and female distributions differ in the early part of the flight season ($\chi^2_{(4)} = 55.97$, $p < 0.001$) and during the latter part of the adult flight period ($X^2_{(4)} = 16.52$, $p < 0.01 > 0.001$). From casual observations, this pattern occurs also during the first brood. Several questions emerge from these observations. Why does the bias in male distribution change systematically from north to south ? Why does an identical pattern not occur in the females ; indeed, why is it that changes in the female distributions appear to be in an opposite direction ?

Two fundamentally different reasons are possible for the gradual shift southwards in the male distribution. First, an increasing number of males

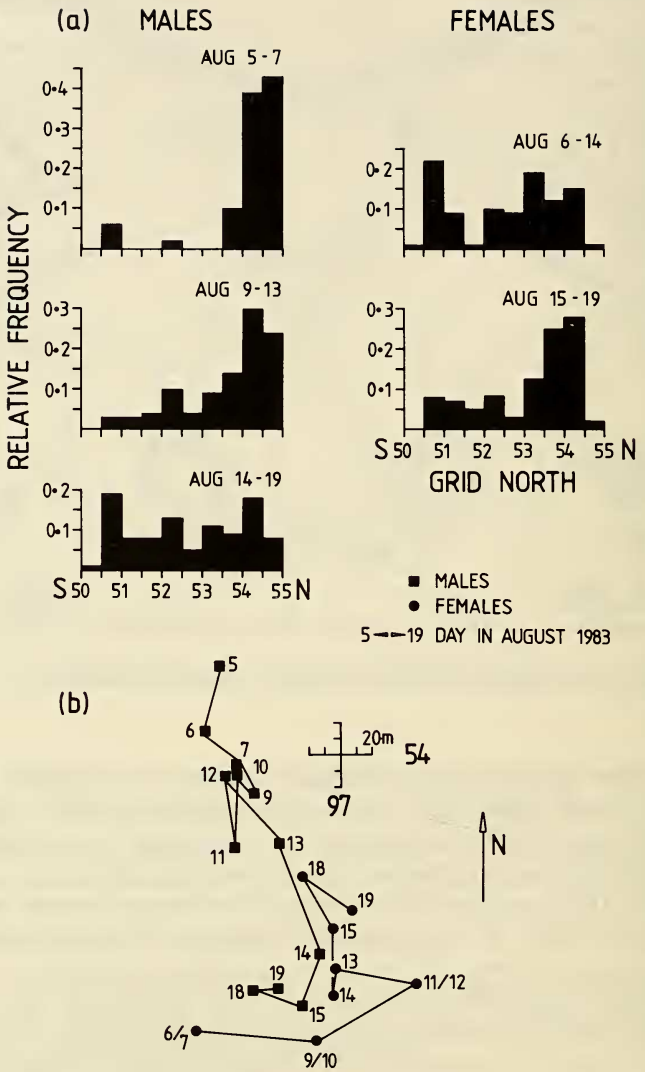

Fig. 5. (a) Histograms illustrating the changes in *L. megera* male and female distributions on Brereton Heath along a north-south axis ; (b) Centroids (mean centres) of distributions for male and female *L. megera* at Brereton Heath on different days for the second brood in 1983. The intersection of easting 97 and northing 54 provide both position and scale.

Table 1
Climatic data and population statistics for male *L. megera* on Brereton Heath from August 5-19, 1983.
The figure for August 5 is a Lincoln index calculation. $\hat{N}_i$, the population size ; $\hat{L}_i$, the number of losses from the population between days i and i + 1 ; $\hat{B}_i$, the number of additions to the population between days i and i + 1. August 8, 16 and 17 had 3.5, 0 and 1 sun hours respectively.

		Fisher/Ford		Jolly		
August	$\hat{N}_i$	$\hat{L}_i$	$\hat{B}_i$	$\hat{N}_i$	°C	Sun Hours
5	(3)	1	–	(3)	17.8	6.8
6	8	2	6	11	20.0	6.0
7	30	8	24	42	21.7	8.0
9	54	15	32	38	23.3	9.3
10	54	15	14	34	21.7	6.0
11	56	15	16	64	22.2	9.0
12	62	17	21	70	22.2	3.5
13	90	24	45	123	18.9	9.0
14	102	27	36	97	22.2	9.5
15	89	24	14	92	27.8	9.0
18	118	32	53	80	22.2	10.0
19	114	31	28	–	25.6	9.0

Survival rate (θ) = 0.733 ; mortality rate (m) = 0.267 ;
Expectation of life (1/m) = 3.7 days ; * $1/\log_e(1\text{-}m)$ = 3.2 days.

may move out as the season progresses. A variety of reasons are possible including the shift in the distribution of resources (i.e., nectar, females) or competition among males as the number flying increases. Secondly, the change in distribution may result from the gradual eclosion of males further south and their fidelity to emergence sites. This would reflect entirely on a climatic difference between the north and south parts of the heath and differences in movement between the sexes. The shift in female distribution, on the other hand, can be due only to movement and a corresponding change in resources or pressures and not to the pattern of eclosion (*vide infra*). The validity of these alternatives depends much on the statistics of movement and local climate.

Movement. Movement statistics have been calculated almost entirely from MRR data, and this undoubtedly introduces a bias inasmuch as recaptures are made within a limited area. The maximum distance that could be recorded would be just over 600 metres. Nevertheless, the data point to very limited movement in the butterfly on the heath. The area studied is some 450 metres^2 yet the average movement for males is much less than this. Only five males were found to have travelled over 300 metres. Indeed, the distance travelled during the average length of stay of 3.2 days (a crude substitute for lifespan) is only some 132 ± 19.1 metres (Table 2). Although the amount

Table 2
Movement statistics for male and female *L. megera*
on Brereton Heath during the period August 5-10, 1983.
R_T, the range between the first and last capture ; R_S, the maximal range. Figures (in metres) including means ($\bar{x}$), standard errors (SE) and daily rates ($\bar{x}$/Days) are quoted for increasing numbers of days insects are known to be in residence (or alive) (days).

Males							Females		
		R_T			R_S			R_S	
Days	$\bar{x}$	SE	$\bar{x}$/Days	$\bar{x}$	SE	$\bar{x}$/Days	Days	$\bar{x}$	SE
0	72.8	7.5	-	77.2	7.8	-	0	90.7	17.1
1	81.4	11.0	81	94.9	10.9	95	1	121.1	35.5
2	92.4	11.0	46	118.9	12.1	59	2 +	216.3	39.2
3	131.8	19.1	44	167.6	18.1	56			
4	84.1	12.0	21	128.7	14.2	32			
5 +	178.7	28.7	27	213.2	25.4	32			

of movement in males increases with their life span, the *rate* of movement decreases and for each daily movement in life, $R_S > R_T$. This corresponds with a Batschelet r of - 0.351 ± 0.065 ($110.6° \pm 3.53°$), indicating a high tendency to turn. All this is in agreement with their observed behaviour ; many males show fidelity to particular zones over several days and patrol back and forth over short distances. Crossmovements between nine zones on the heath demonstrate more effectively that the shift in the male distribution is not due to the movement of adults southwards (Figure 6). Not one individual captured in the north west paddock (zone 2) was recaptured in the south. A large percentage of recaptures are made in the same zone. Most movements occurred between the paddock and the adjoining lake margin and road. Many individuals entered the paddock in the early evening to roost under the fencing. There is some evidence that inter-male competition (skirmishes) is responsible for retaining much the same number in the paddock from day to day. After a short period of vacancy and within half an hour of the capture and incarceration of all males within the paddock, numbers are restored to the same level as before. Female movements are greater but apparently not significant so. However, the sample of female recaptures is totally inadequate for any firm conclusions to be made and it is suspected that this reflects losses from the population by outmovement as much as differences in behaviour. Of course, all the above does not deny the existence of long distance outmovements. The butterfly has been commonly seen in suburban gardens during the drought of 1984 ; therefore numbers of butterflies evidently leave their sites of eclosion. This is by no means the only species for which contradictory observations have been made on individual movements (see Baker 1978, Courtney 1980 and Dennis (in press) for *A.*

cardamines; and BAKER 1978, POLLARD 1981, BRAKEFIELD 1982 and FORD 1957, 1975 for *M. jurtina*).

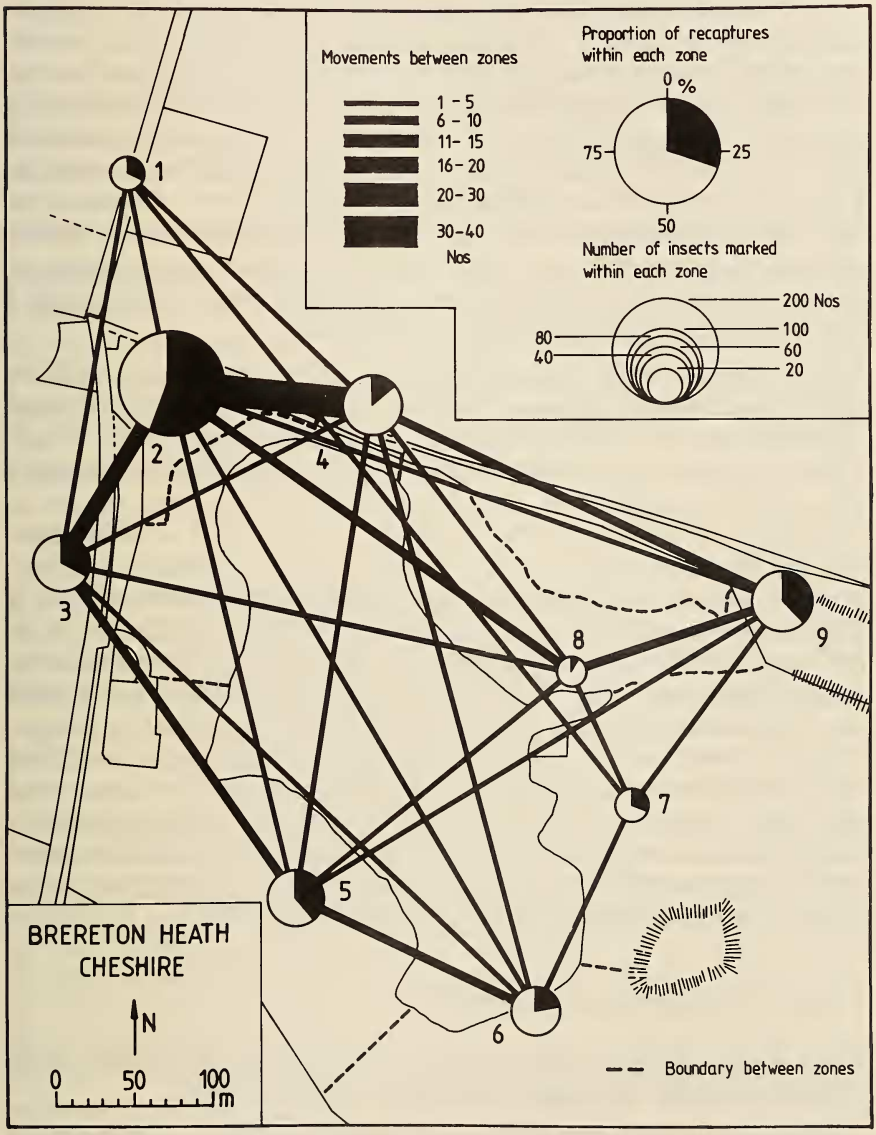

Fig. 6. Movement of male *L. megera* between nine zones on Brereton Heath, for the period August 5-19, 1983, illustrating the number of captures, the percentage of recaptures occuring within areas of prior capture and the degree of interchange between zones.

Climate. Distinctive climatic contrasts occur on the heath. Exposed areas, particularly the eastern bank of the lake and the opening to the car park, have the highest windspeeds, whereas the western paddock, the sheltered horse run and western enclaves in the woodland have the lowest figures. Temperatures taken on August 25, 1983 demonstrate that the north bank is warmer than the south bank on average by 1.2°, despite higher wind speeds on the north bank due to an atypical southerly wind on that day. The differences is significant for exposed ($t_{(8)} = 4.2$, $p < 0.001$) and shade temperatures ($t_{(9)} = 4.74$, $p < 0.01$) and for much of the day, the shade temperatures in the north are higher than exposed temperatures in the south. Conditions in the north west paddock are noticeably warmer still because of the shelter afforded by surrounding trees. These conditions evidently occur throughout the year, as snow cover in the northern part of the heath is always melted before that in the south (Ainsworth, pers. comm.).

On the whole, therefore, despite the potential for long distance dispersal, the shift in male distribution seems to relate to a gradual pattern of emergence southwards on the heath, individuals further south taking longer to pass through immature stages. Males emerge first in the north and congregate in the north west paddock. As numbers rise there is some outmovement to adjoining areas, but many individuals return to roost. There is some indication that the paddock loses some of its advantage as the season progresses, probably, because more females emerge at a greater distance from it and it therefore lies beyond their sensory range but also because sufficient males by that stage are eclosing nearby anyway. The inverse pattern of movement in females seems most easily related to concentrations of males. Once females have been mated they move out of the orbit of male harassment to lay eggs. Thus in the early part of the flight period they are found further south than the male distribution and in the latter part further north. It is unlikely that the overall distribution of nectar sources controls the changing pattern of adult dispersion as these were numerous, varied and freshly available over the heath during the flight season. Only in the sandy east paddock are nectar sources likely to dessicate in a hot dry season as in 1984.

3. Long term changes in distributions

Much of the long term distribution of *L. megera* on Brereton Heath relates to land use, but by no means is all human influence negative.

Positive influences : Prior to being a sand quarry the lightly wooded heathland must have been unproductive for butterflies, few of the present species occurring there. The quarry opened up the woodland, allowed a range of hostplant and nectar adventives to enter and is the reason for the variety of

butterflies there now. The value of the site for butterflies has increased further with the closure of the quarry and its promotion to a country park. Nectar sources and larval hosts have increased in variety with the termination of sand extraction. Maintenance of the open area by the ranger, walkers, horseriders, fishermen and rabbits have all been beneficial to *L. megera*; bare areas of ground are retained as perch sites for males and scrub invasion held at bay. The demarcation of the horse run and paddocks has also been valuable ; the fencing is used for roost sites ; horse tracks in the soft ground of the east paddock provide innumerable egglaying sites and the track a flyway and perch sites for males. Maintenance and addition of shrubs and trees to the heath surround give vital shelter and increase the warmth of the heath.

Negative influences: Typically negative land uses are the car park, newly created in 1982 (to be extended to the south into the woodland in 1985) ; the mown grass areas (not entirely negative as some nectar is occasionally available, — hawkweeds and clover) and the main recreation zones. Several hundred visitors arrive on hot summer days, the parked vehicles extending the full length of the adjoining road, but thankfully, visitors are usually gregarious and concentrate in two areas (Figure 1).

Conclusions

L. megera prefers warm sunny sheltered sites, particularly edge sites and those on broken ground. The sheltered south facing west paddock and the north bank are far more favourable to the butterfly than other sections of the heath. This is evident from the total number of males in these areas compared to other parts of the heath (Figure 6). Butterflies artificially released in the south have a short 'stay' time and recaptures within the southern zone are fewer than anywhere else, except the exposed east bank (zone 8). These observations point to reasons for the limit to the distributions of the insect in Britain. Summer temperatures decrease with altitude and to the north. Not only are high temperatures required by males for effective mate location activity and by females for egglaying, but early stadia evidently grow slowly in lower temperature regimes and the development of the second brood probably becomes critical near the Scottish border (see HEATH *et al.* 1984, p. 119). Late emerging adults will not only be fewer because of the increased times over which predators and parasites have operated on them (cf. POLLARD 1979), but will have reduced success in mating and oviposition as colder autumn conditions set in. The resultings eggs and larvae may develop too slowly to survive the winter. The distribution along the coast relates to lower altitude and higher temperatures but probably also to drier summer conditions ; in this situation, higher windspeeds may benefit *L. megera* as the ground will dry more rapidly and warm up as a result.

When climatic conditions improve, *L. megera* is among those British butterflies best suited to extending its range. This is probably because eggs are laid *under* hedges thereby escaping better the frequent artificial cuts and treatment with herbicides. Not only that, but the insect also uses hedges and field corners as a mate location cue unlike many other Satyrids and is opportunistic in exploiting a wide array of nectar sources surviving grass verge control. In this way, it is one of the few species in Cheshire that can spread out from preferred habitats suchs as Brereton Heath.

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